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Published in:
PeerJ

DOI:
10.7717/peerj.5634

Published: 28/09/2018

Document Version
Peer reviewed version

Functional responses of a cosmopolitan invader demonstrate intraspecific variability in consumer–resource dynamics

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Running headline: Functional responses of a global invader

ABSTRACT:

Background. Variability in the ecological impacts of invasive species across their geographical ranges may decrease the accuracy of risk assessments. Comparative functional response analysis can be used to estimate invasive consumer–resource dynamics, explain impact variability, and thus potentially inform impact predictions. The European green crab (*Carcinus maenas*) has been introduced on multiple continents beyond its native range, although its ecological impacts appear to vary among populations and regions. Our aim was to test whether consumer–resource dynamics under standardized conditions are similarly variable across the current geographic distribution of green crabs, and to identify correlated morphological features.

Methods. Crabs were collected from multiple populations within both native (Northern Ireland) and invasive regions (South Africa and Canada). Their functional responses to local mussels (*Mytilus* spp.) were tested. Attack rates and handling times were compared among green crab populations within each region, and among regions (Pacific Canada, Atlantic Canada, South Africa, and Northern Ireland). The effect of predator and prey morphology on prey consumption was investigated.

Results. Across regions, green crab consumed prey according to a Type II (hyperbolic) functional response curve. Attack rates (i.e., the rate at which a predator finds and attacks prey), handling times and maximum feeding rates differed among regions. There was a trend toward higher attack rates in invasive than in native populations. Green crabs from Canada had lower handling times and thus higher maximum feeding rates than those from South Africa and Northern Ireland. Canadian and Northern Ireland crabs had significantly larger claws than South African crabs. Claw size was a more important predictor of the proportion of mussels killed than prey shell strength.

Discussion. The differences in functional response between regions reflect observed impacts of green crabs in the wild. This suggests that an understanding of consumer–resource dynamics (e.g., the *per capita* measure of predation), derived from simple, standardized experiments, might yield useful predictions of invader impacts across geographical ranges.

INTRODUCTION

The ever-increasing rate of introductions of species beyond their native ranges and the potential negative impacts on native biodiversity of species that become invasive continue to generate worldwide concern (Seebens *et al.* 2017). However, the effects of invaders are notoriously difficult to predict, especially across geographical ranges (Simberloff *et al.* 2013; Doherty *et al.* 2016). Many predatory invaders are responsible for large declines in the abundance and richness of native species (e.g., Wiles *et al.* 1995; Medina *et al.* 2011). These impacts are often attributed to advantages of invasive predators in novel environments, including the lack of prey resistance, release from natural enemies/pathogens, or behavioural, morphological, and physiological pre-adaptations (Alpert 2006; Sih *et al.* 2010; Weis 2010; Roy *et al.* 2011). However, not all introduced predators cause notable declines in native populations (Gurevitch & Padilla 2004; Zenni & Nuñez 2013); some have minimal detectable impacts on recipient ecosystems (Simberloff & Gibbons 2004; Hampton & Griffiths 2007; Howard, Therriault & Côté 2017). These variable outcomes may arise because the impacts of an invasive predator are influenced by context-specific biotic and abiotic conditions (Lipcius & Hines 1986; Alcaraz, Bisazza & García-Berthou 2008; Robinson, Smee & Trussell 2011; Barrios-O'Neill *et*

71 *al.* 2014; Paterson *et al.* 2015). This variability can make it difficult to accurately predict the
72 impacts of invasive species (Dick *et al.* 2017), especially when the same invasive species occurs
73 at multiple locations (Melbourne *et al.* 2007; Kumschick *et al.* 2015).
74 Comparative functional response analysis (CFRA) has become a useful tool for
75 elucidating relative variability in consumer–resource interactions among invasive species and
76 under different contexts (Barrios-O'Neill *et al.* 2014; Alexander *et al.* 2015; Paterson *et al.* 2015;
77 Dick *et al.* 2017). The functional response is the relationship between consumer (e.g., predator)
78 consumption rate and resource (e.g., prey) density (Holling 1959, 1965). This relationship
79 provides information on the ability of a predator to find and consume prey and, by extension, its
80 potential ecological impacts (Dick *et al.* 2013). Unlike predation studies, which seek to directly
81 measure the impact of an invasive species in a particular location or on a particular species, the
82 CFRA approach uses simplified experimental conditions to generate relative (not absolute)
83 parameters that are comparable across contexts. Functional responses can be linear (Type I),
84 hyperbolic (Type II), or sigmoidal (Type III) (Holling 1965). The magnitude and type of
85 functional response can determine predator–prey coexistence (Holling 1959; Oaten & Murdoch
86 1975; Hassell 1978). Type II responses in particular may potentially destabilize prey populations
87 and lead to localized prey extinction (e.g., Lipcius & Hines 1986; Rindone & Eggleston 2011;
88 Spencer, Van Dyke & Thompson 2016). Studies using CFRA have consistently demonstrated
89 that invasive species, ranging from plants (Funk & Vitousek 2007) to invertebrates (Dick *et al.*
90 2013) and vertebrates (Alexander *et al.* 2014), consume available resources at a higher rate than
91 analogous native species. While these results support the general concept that successful invasive
92 species do well, in part, because they are more efficient at using resources, context-dependent
93 biotic interactions or abiotic conditions can cause variation in invasive species functional

responses (Barrios-O'Neill *et al.* 2014, 2016; Paterson *et al.* 2015). It is thus unclear whether we should expect the functional responses of an invasive species to be conserved across geographical ranges or whether context differences between populations will result in variable functional responses. Intraspecific geographic comparisons of functional responses should make it possible to estimate the relative importance of local behavioural and morphological adaptations in determining invader responses to resource availability and their potential ecological impacts.

The European green crab (*Carcinus maenas*) is a well-known invasive species that occurs in intertidal and shallow subtidal habitats around the world (Behrens Yamada 2001) (Fig. 1). Green crabs are viewed as highly effective generalist predators (Gillespie *et al.* 2007), with detrimental effects for native biodiversity in some regions (Welch 1968; Walton *et al.* 2002; Matheson *et al.* 2016). However, there is large variation in the reported impacts among green crab populations, which does not simply relate to time since invasion. For example, on the east coast of North America, where green crabs have been established since the 1800s (Say 1817), significant declines in commercially important shellfish stocks have been attributed to green crab predation (Glude 1955; Welch 1968). There are also notable ecological impacts on shellfish species on the west coast of North America, where green crabs have been established since the 1990s (Grosholz *et al.* 2000, 2011). In contrast, there are limited observed impacts by populations in both Australia (introduced 1880s) and South Africa (introduced 1980s) (Fulton & Grant 1902; Le Roux, Branch & Joska 1990; Carlton & Cohen 2003; Hampton & Griffiths 2007; Mabin *et al.* 2017).

In this study, we investigate variability in consumer–resource dynamics of green crabs from regions within both their invasive and native ranges using CFRA. If green crab functional responses are variable among regions, we expect these differences to reflect local ecological

impacts, as demonstrated in interspecific CFRA studies (e.g. Dick *et al.* 2013; Alexander *et al.* 2014; Paterson *et al.* 2015). Thus, crabs from populations within regions should have similar functional responses, but crabs from North American regions (in this study, Atlantic and Pacific Canada) might be expected to have higher functional responses than those from regions within the native range (in this study, Northern Ireland) and parts of the invaded range where their impacts appear limited (in this study, South Africa). We also investigated morphological differences among both crab and prey populations that might potentially cause inter-regional differences in functional responses.

MATERIALS AND METHODS

Site selection and animal collection

Green crabs were collected from nine populations from four regions where green crabs have been introduced: British Columbia, Pacific Canada (BC, n = 2 populations), Nova Scotia, Atlantic Canada (NS, n = 2), and South Africa (SA, n = 2), and from the region where they are native: Northern Ireland, UK (NI, n = 3) (Fig. 1). A minimum of 18 crabs were collected from each site between July and September 2014 (Table S1). All crabs collected were males, with carapace widths between 55.0 and 65.0 mm, intact claws, and a firm shell (as springy or soft shells indicate recent moulting). Although the invasive congener *C. aestuarii* was previously recorded as co-occurring in very low densities alongside *C. maenas* in South Africa in the mid 1990s, they were no longer present a decade later (Robinson *et al.* 2005, 2016). As such, all

South African crabs were correctly identified as European green crab. Intertidal mussels of the genus *Mytilus* (BC: *M. trossulus*; NS: *M. edulis*; NI: *M. edulis*; SA: *M. galloprovincialis*) were used as prey because they are widely available in all four regions (Gosling 1992), are readily consumed by green crabs (Elner 1981; Morton & Harper 2008; Behrens Yamada, Davidson & Fisher 2010), and are ecologically similar to one another (Seed & Suchanek 1992). Mussels of 25 mm (± 3 mm) length were collected by hand from a single site in each region, which standardized prey across populations within region. A similar standardization (i.e., using the same prey species) was not possible across regions, owing to ethical concerns about non-native species introductions.

Animals were housed in local research laboratories (BC: Bamfield Marine Sciences Centre; NS: Bedford Institute of Oceanography; NI: Queen's University Belfast; SA: Stellenbosch University). All crabs were housed in indoor tanks, with artificial lighting on day/night cycles similar to local summer conditions. In BC and NS, tanks were supplied with flow-through seawater from adjacent inlets. Tanks in SA and NI used artificial seawater systems. Across all trials, water temperatures varied across a narrow range (9 - 15 °C) suitable for green crab feeding (7 - 26 °C, Behrens Yamada 2001). Salinity range (30 - 36‰) was also well within green crab tolerances (4 - 54‰; Behrens Yamada 2001). Prior to and after being used in experiments, crabs in all locations were fed raw bait fish (e.g., herring) every two to three days. Prey animals were held separately from green crabs but under similar conditions.

Experimental set-up and methods

At all locations, we used plastic bins (61 cm long x 40.6 cm wide), filled with seawater to a depth of 23 cm, as experimental chambers for all trials. The lids had a mesh screen to prevent escape while allowing light to diffuse inside the bins.

Prior to trials, green crabs were isolated and starved for 48 h to standardize hunger levels. Each crab was used only once. Intact mussels were cleaned of encrusting biota and checked for pre-existing damage. The evening prior to a trial, each bin received a randomly assigned prey density of 2, 4, 8, 16, 32, or 64 mussels, which were scattered across the bottom. The following morning, a single crab was placed into each bin and allowed to forage for eight daylight hours. Each prey density was replicated three times for each of the nine green crab populations tested. We retained, fed, and monitored all crabs for one week after testing to ensure that feeding behaviour had not been affected by imminent moulting. Because no moulting was observed, crabs that had eaten no prey (BC = 1/36 trials, NS = 2/35 trials, SA = 6/36 trials, NI = 15/54 trials) were retained in the analysis to reflect individual variation, and because reduced consumption at low prey densities can be indicative of a Type III functional response. One Nova Scotia trial (at prey density = 2) was omitted owing to crab mortality. One predator-free control bin was run for every prey density and region to measure mussel mortality unrelated to predation.

Morphological measurements

We evaluated morphological characteristics of both predator and prey that could cause differences in functional responses among populations. Claw size in green crabs is known to vary among populations (Smith 2004; Schaefer & Zimmer 2013), and claw strength is directly

proportional to claw size, which has implications for handling times of crabs consuming shelled prey (Behrens Yamada *et al.* 2010). We therefore measured crusher claw propal height as an index of claw size for each crab (Behrens Yamada & Boulding 1998). Similarly, mussel shell thickness could influence consumption by green crab. We did not measure shell thickness of mussels in each trial, as mussels that were not consumed may have been rejected due to their thickness. Instead, in each region we collected an additional 19 to 30 randomly selected mussels of the same size as used in the trials, euthanized them and removed the tissue, keeping the valves intact. Shells were air-dried, measured and weighed to the nearest 0.01 g. Following Freeman, Meszaros and Byers (2009), we calculated the shell thickness index (*STI*) as:

$$STI = Shell\ weight/[L * (H^2 + W^2)^{0.5} * \pi/2]$$

where *L*, *H*, and *W* correspond to linear measurements (in mm) of shell length (maximum anterior-posterior axis), height (maximum dorsal-ventral axis), and width (maximum lateral axis), respectively (Lowen, Innes & Thompson 2013).

Analysis

All analyses were done using R version 3.3.2 (R Development Core Team 2008). Data were tested for homogeneity of variances and normality prior to statistical analyses to determine possible regional differences. The carapace width data were non-normal so a Kruskal-Wallis test was used, and the claw size data were heteroskedastic, and thus a Welch's F test was used. We examined the relationship between the number of prey killed and average temperature (i.e., start

temperature + end temperature/2) across all 64-mussel trials, using a linear mixed-effect model with region as a random effect. Temperature did not explain a significant amount of variation in number of mussels killed (Likelihood ratio test: $X^2 = 0.618$, df = 1, $P = 0.43$; Fig. S1). We therefore did not consider temperature in further analyses.

To determine functional responses as Type II or Type III, we first fit the proportion of prey consumed to prey density for each population using a logistic regression with the package 'frair' (frair::frair_test). Because the logistic regressions generated negative first-order terms in all cases, indicative of Type II functional responses (Juliano 2001), we then fit the data using the appropriate random predator equation (see Results), without prey replacement (Rogers 1972):

$$N_e = N_0(1 - \exp(a(N_e h - T)))$$

where N_e is the number of prey eaten, N_0 is the starting prey density, a is the attack rate, h is the handling time, and T is the experimental duration. Values of N_e and N_0 were generated experimentally, while a and h were estimated by fitting the model. Models were fit for each population using maximum likelihood estimation with the package function frair::frair_fit and bootstrapped (n = 2000) to generate 95% confidence intervals.

Because functional responses were similar within regions (see Results, Figs. S2 and S3), we pooled populations within regions to test whether inter-regional differences were driven by differences in attack rate (a) or handling time (h). We re-fitted Rogers' Type II curves to regional data and bootstrapped the fits (n = 2000) to generate parameter estimates for a, h and maximum feeding rates ($1/hT$). The 95% confidence intervals for these parameter estimates were first compared visually and then more formally where necessary (Table S2).

Finally, to identify factors underpinning regional differences in prey consumption, we used generalized linear mixed-effects models (GLMMs) with a binomial error distribution to predict the proportion of prey consumed by green crabs as a function of claw size, prey STI, and region using a suite of additive candidate models. Mean prey STI for each region was included as a continuous, fixed effect. Because attack rates and handling times by green crabs from both Canadian regions (see Results) were similar, we combined BC and NS into a single region (North America, NA) for comparison with SA and NI. Finally, we included initial prey density as a fixed effect – not as an explanatory variable *per se* but because it is important in functional responses – and population as a random effect in all candidate models. The best-supported model was identified using Akaike's Information Criterion corrected for small sample sizes (AICc), where the top model had the lowest AICc value (Burnham & Anderson 2002). We also determined the relative variable importance (RVI) of each fixed effect, based on the sum of the AICc weights for models that included the focal variable (Burnham & Anderson 2002), and the marginal and conditional R^2 values for the top model (Nakagawa & Schielzeth 2013). To display the individual effect of each variable included in the top model on the predicted proportion of mussels killed, we used the 'effects' package to calculate effect sizes for each variable, relative to the mean values (continuous data) or proportional distribution (categorical data) of the other factors in the model (Fox 2003, Fox & Hong 2009).

RESULTS

Regional patterns of functional responses

In trials without crabs, 100% of mussels survived. All logistic regressions indicated the predation data were best fit using Type II functional response models. Within regions, the confidence intervals around the number of prey killed overlapped between populations at most prey densities, indicating that differences in predatory behaviour within regions were minimal (Figs. S2 and S3). Inter-regionally, we found the highest functional response curves for North American green crab (BC and NS) (Fig. 2). Attack rates (*a*) were highest in BC, NS, and SA and the lowest in NI, but there was overlap in confidence intervals between all regions except BC and NI and NS and NI (Fig. 3a, Table S2). Handling times (*h*) were lower in BC and NS than in SA and NI, with no overlap of confidence intervals between these two groups (Fig. 3b, Table S2). By extension, the maximum feeding rates of North American green crabs were considerably higher than those of crabs in SA or NI (Fig. 3c).

Potential drivers of regional variation in prey consumption

Although there was no significant difference in crab carapace width among regions (Kruskal-Wallis test, $P = 0.68$), claw size did differ significantly among regions (Welch's $F_{3,84.55} = 40.28$, $P < 0.01$), with crabs from NI, BC and NS having the largest claws and those from SA, the smallest (Fig. 4a). Mussel shell thickness index (STI) also differed significantly among regions (Kruskal-Wallis test, $P < 0.01$), resulting in a clear regional ranking (SA>NI>BC>NS) of decreasing mussel shell thickness (Fig. 4b).

Prey density was the most important variable (RVI = 1.0) and was included in all models of proportion of prey consumed by green crabs. Region (RVI = 0.98), claw size (RVI = 0.85) were the next most important variables across all models. Prey STI (RVI = 0.48) was relatively less important.

There was substantial support for two of the candidate models (Table 1). Both included claw size and region as important predictors of the proportion of mussels killed. The second-ranked model also included prey STI, but this variable had poor explanatory power: it did not substantially improve the model fit (as indicated by the log-likelihood) or the marginal R^2 (Table 1).

The variables in the top model were prey density, claw size, and region (Table 1). Increasing prey density resulted in proportionally fewer mussels being killed, as expected from Type II functional responses that reach saturation (Fig. 5a). The proportion of mussels killed increased with claw size, as expected, regardless of region and prey density (Fig. 5b). At mean prey density and claw size, mussels had a 33% chance of being killed by green crabs in NI and SA (Fig. 5c). In contrast, and as predicted, green crabs in North America imposed the highest prey mortality. The probability of a mussel being killed in North America was 67% (Fig. 5c). Together, these three fixed effects in the top model explained 29% of variation in the proportion of prey killed (marginal R^2). The combination of the fixed effects and random effect (population) explained 31% of this variation (conditional R^2). To validate our approach of combining the North American populations we also re-ran the analysis on a modified version of our top model that included all four regions, rather than three, to see if there were any differences in the results. All the trends were consistent with our top model (Fig. S4), and there were no differences in the marginal and conditional R^2 values or the model coefficients for prey density and claw size.

DISCUSSION

Comparative functional response analysis (CFRA) has consistently demonstrated that the functional responses of invaders reflect their known ecological impacts, but it has traditionally focussed on interspecific comparisons between invasive and native species (e.g., Dick *et al.* 2013; Alexander *et al.* 2014; Paterson *et al.* 2015). CFRA has not previously been used to investigate geographic variation in functional responses of a single, cosmopolitan invader. Here, we did not observe large differences in the functional responses of green crabs from populations within regions: Although it cannot be assumed our results apply to entire ranges, as this would require more extensive sampling in both North America and Europe, crabs from populations several hundred kilometres apart but in the same region showed similar attack rates, prey handling times, and maximum feeding rates. However, differences in functional response curves and parameters among regions were large. Furthermore, the higher functional responses of invasive green crabs from North America compared to South Africa and Northern Ireland appear to reflect, at least qualitatively, their predatory impacts in the wild (see Glude 1955; Welch 1968; Grosholz *et al.* 2000, 2011, Mabin et al 2017). Despite their experimental simplicity, functional responses might therefore be a useful, relative estimate of predation that can help inform predictions about the ecological impacts of green crabs in areas where more refined impact predictions are not yet available or impossible to make.

We found regional differences in green crab capacity to kill mussels. These differences stemmed mainly from differences in handling times, and by extension maximum feeding rates (which are mathematically derived from handling times), although some variation in attack rates was also observed. The foraging success of predators depends on their behaviour, morphology, and physiology as they detect, attack, capture, and consume prey (Hassell 1978; Lima 2002).

Attack rate (*a*) reflects the first two steps of this foraging sequence. We found some inter-regional differences in attack rates, with invasive crabs from BC demonstrating higher attack rates than those in Northern Ireland. Handling time (*h*), by comparison, reflects the time it takes for a predator to capture and consume prey items and is influenced by physiological and morphological constraints on the predator (Elner & Hughes 1978; Hassell 1978; Vucic-Pestic *et al.* 2010). Handling times were markedly lower, and maximum feeding rates (1/*h*T) higher, for green crabs from North America than for those from South African and Northern Ireland. Interestingly, higher resource consumption by invasive species, compared to native species, is usually realized either through higher attack rates (e.g., Dick et al. 2013) or lower prey handling times (e.g., Bollache *et al.* 2008; Haddaway *et al.* 2012; Alexander *et al.* 2014), but rarely both. Differences in attack rates among regions might have been driven by differences in individual activity levels, which are often higher in invasive than in native species (Sih, Bell & Johnson 2004). In contrast, differences in claw size likely drove the observed differences in handling times. Green crabs from North America (BC and NS) had significantly larger claws, and shorter handling times, than crabs from South Africa. Crabs with larger claws have a morphological advantage over crabs with smaller claws, because large claws reduce the effort required to break mussels and the risk of claw damage (Behrens Yamada *et al.* 2010). This suggests that invasive green crabs from North America are morphologically better suited to handling hard-shelled prey than those from South Africa. Contrary to the pattern, however, native green crabs in Northern Ireland had large claws, on par with those of North American green crabs, but their handling times were significantly lower, more closely matching those seen in South African crabs. Because handling time incorporates both breaking time and eating time (Elner & Hughes 1978; Lee & Seed 1992; Smallegange & van der Meer 2003; Calderwood *et al.* 2016), perhaps crabs in

345 Northern Ireland are under less pressure to ‘eat quickly’ due to less competition or
346 kleptoparasitism (Smallegange, van der Meer & Kurvers 2006; Chakravarti & Cotton 2014),
347 while still requiring large claws to crush thick-shelled local mussels.
348 There are four possible explanations for inter-regional differences in claw size and prey
349 handling times. First, differences could be primarily driven by genetic variation. While there are
350 detectable founder effects in some green crab populations (Darling *et al.* 2008), genetic variation
351 does not explain the large phenotypic variation seen, including in claw size, within the native
352 range of green crabs (Brian *et al.* 2006). It therefore seems unlikely that inter-regional variation
353 in claw size is linked to a variable genetic make-up of founder individuals. Second, claw size
354 could be a highly plastic trait. Green crabs can modify their claw sizes in response to prey shell
355 thickness (Brian *et al.* 2006; Schaefer & Zimmer 2013). This phenotypic response occurs under
356 laboratory conditions (Baldridge & Smith 2008) and along biogeographic gradients (Smith
357 2004). In our study, claw size did not covary with prey shell thickness. However, the
358 standardized mussel prey we offered might have not always reflected local diets of green crabs.
359 For example, green crabs in British Columbia are currently only found in soft-sediment habitats
360 where their diet consists mainly of infaunal clams (Klassen & Locke 2007), which can have very
361 thick shells (Boulding 1984). In contrast South African green crabs eat predominantly small
362 gastropods and soft-bodied prey (e.g., polychaetes) (Le Roux *et al.* 1990). Claw size may
363 therefore normally be more closely linked to prey characteristics than our results suggest. Third,
364 differences in water temperatures could affect the calcification of crab exoskeletons and of their
365 molluscan prey. Warmer temperatures lead to decreased calcification, so crabs in warmer
366 habitats may therefore have weaker claws with which to attack shelled prey. However, because
367 the effect of decreased calcification would also make prey shells weaker handling times should

368 be unaffected overall (Landes & Zimmer 2012). Finally, inter-regional variation in claw sizes,
369 and by extension handling times, may reflect selective forces beyond prey defenses, including
370 reproduction (mate competition) and agonistic interactions (interference competition) (Lee &
371 Seed 1992). Claw size is the best determinant of success in intra- and interspecific agonistic
372 interactions between crabs (Lee & Seed 1992; Sneddon, Huntingford & Taylor 1997). It is
373 notable that green crabs in North America face competition from large-clawed decapods like
374 Dungeness crab (*Metacarcinus magister*) in BC and American lobster (*Homarus americanus*) in
375 NS (McDonald, Jensen & Armstrong 2001; Rossong *et al.* 2006). A combination of exposure to
376 thick-shelled prey and a highly competitive environment could explain the especially large claws
377 and fast handling times of green crabs sampled from North America compared to those from
378 other populations.
379 Globally, the impacts of green crabs seem to vary among regions, with some populations
380 (e.g., North America and Tasmania) appearing to have larger impacts on intertidal communities
381 than others (e.g., South Africa, Australia, or Japan) (Behrens Yamada 2001). The quantitative
382 evidence for this variability is provided by a few large-scale field studies showing that green
383 crabs are effective bivalve predators that have negatively impacted native community
384 composition, trophic interactions, critical habitat, and human economic interests (Welch 1968;
385 Grosholz *et al.* 2000; Walton *et al.* 2002; DeRivera, Grosholz & Ruiz 2011; Matheson *et al.*
386 2016). Our finding that green crabs sampled from North America have higher attack rates and
387 lower prey handling times than those sampled from other regions is consistent with these field
388 observations. Moreover, North American green crabs have had markedly different patterns of
389 spread than in other regions, including in South Africa where green crabs have a comparatively
390 restricted range despite becoming established decades ago (Mabin et al. 2017). The limited

391 success and impacts of invasive green crabs in South Africa has been attributed to abiotic
392 conditions (e.g., fast-flowing water and highly exposed coasts) being unfavourable to range
393 expansion (Le Roux *et al.* 1990; Robinson *et al.* 2005; Hampton & Griffiths 2007). Our results
394 demonstrate that South African green crabs exploit a similar prey less effectively than green
395 crabs from other invasive regions. This suggests that the variable success of different populations
396 of green crabs is partially driven by biotic interactions, not just habitat suitability.
397 The CFRA approach has been successful because it entails an extreme reduction of the
398 complexity of experimental conditions. Functional response studies do not seek to generate
399 absolute values of foraging parameters under realistic environmental and other contexts (e.g.,
400 habitat structure). Instead, the approach generates relative parameters that are comparable across
401 species and contexts. Thus, high-impact invasive species typically display functional response
402 curves that are steeper and/or have higher asymptotes than similar native species or lower-impact
403 invaders (e.g., Dick *et al.* 2013; Alexander *et al.* 2014; Paterson *et al.* 2015). Our study is the
404 first to establish that there is also marked inter-regional variation in the functional responses of a
405 globally invasive consumer that appears to reflect, at least qualitatively, the regionally variable
406 impacts of green crabs.
407
408 **CONCLUSIONS**
409 CFRA can be a powerful approach with which to compare the relative impacts of
410 invasive consumers both within and among species. As it relates to European green crab, it
411 would be interesting to apply the method used here to populations of green crab we were not able
412 to cover, such as those in Australia, the more southern parts of the North American ranges, and
413 elsewhere in the native range. This method could also be applied to native decapod species that

co-occur with green crab to help identify how much competition influences foraging behaviours. Finally, while we make the inference that the functional responses described here may reflect impacts of green crabs in the field, data gaps in the literature make it difficult to be more definitive about that relationship or use these functional response results predictively. Methods to link experimental functional responses to field impacts exist (e.g., Parker et al. 1999; Dick et al. 2017), but at a minimum require data on abundance that is largely unavailable for European green crab. Where this information is available, functional responses offer a simplified, standardized metric of *per capita* impact that can be used to predict the ecological impacts of invasive species.

Acknowledgements. We thank Anthony Ricciardi and Josie Iacarella for their input in the development of the question and approach. BRH thanks Claudio DiBacco and Jennifer Fitzgerald for their hospitality, and Sarah Calbick, Nate Feindel, Chris McCarthy and Sean Godwin for their assistance.

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700 Figure 1 Global distribution of European green crab (Carcinus maenas) and sampling locations for
701 green crab populations used in this study. Native (black) and invaded (dark grey) ranges of European
702 green crab (Carcinus maenas). Locations where green crabs occur in isolated populations are indicated
703 by black dots. Open circles indicate locations where green crabs have been collected but established
704 populations are not yet known to exist (see Carlton & Cohen, 2003 for additional details). Insets show the
705 sampling locations (black dots) for populations of green crabs used in this study: BC (British Columbia,

Canada), NS (Nova Scotia, Canada), SA (South Africa), and NI (Northern Ireland, UK). White diamonds indicate locations of major cities near sampling locations.

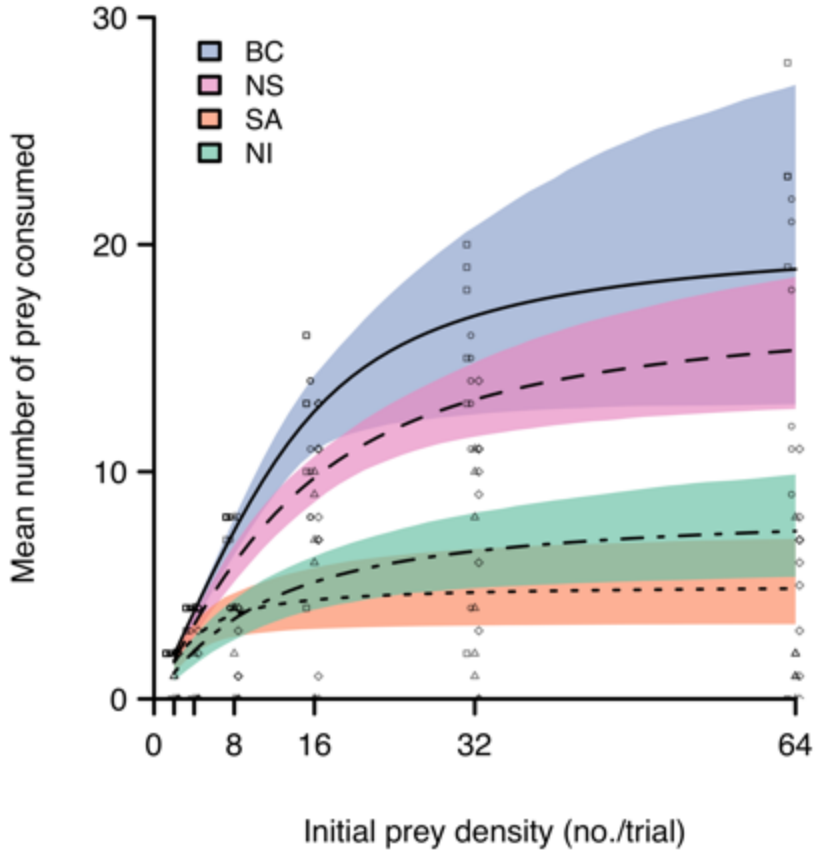

Figure 2 Functional response curves for European green crab preying on mussels (Mytilus spp.) in four regions. Functional response curves, modeled from the raw data (open symbols) with a Type II Rogers random predator equation without prey replacement, for European green crab preying on mussels (Mytilus spp.) in four regions: BC (British Columbia, Pacific Canada; solid line; open square), NS (Nova Scotia, Atlantic Canada; dashed line; open circle), SA (South Africa; dotted line; open triangle), and NI (Northern Ireland, UK; dot-dashed line; open diamond). The mean number of prey consumed by green crab in each region has been averaged across the multiple populations shown in Fig. S3. Shaded areas represent the 95% bootstrapped confidence intervals.

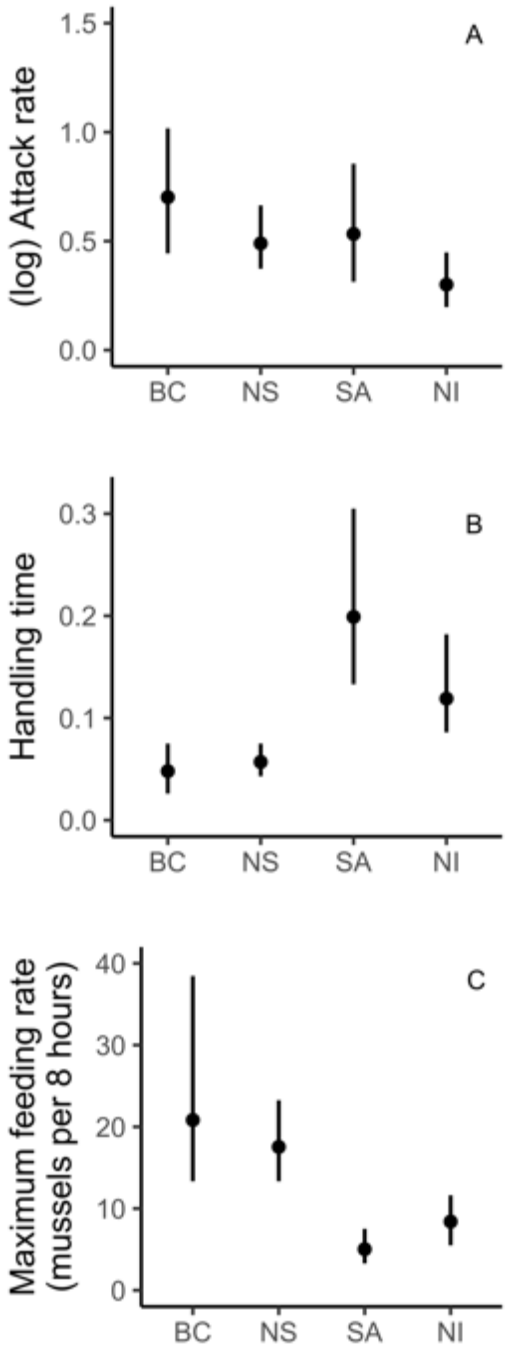

Figure 3 Parameter estimates of attack rate a, handling time h, and maximum feeding rate 1/h T for European green crabs feeding on mussels. Parameter estimates (_95% CI) of (A) attack rate a, (B) handling time h, and (C) maximum feeding rate 1/h T, from bootstrapped Type II functional response curves of green crabs preying on varying densities of mussels. Green crabs were collected from BC (British Columbia, Pacific Canada), NS (Nova Scotia, Atlantic Canada), SA (South Africa), and NI (Northern Ireland, UK.)

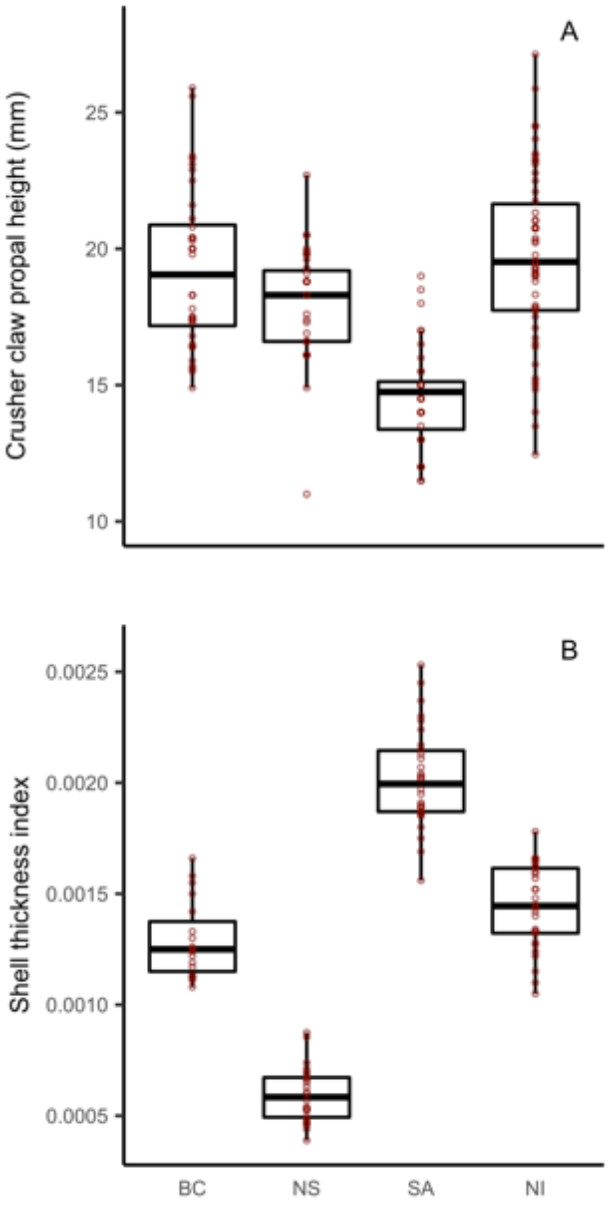

Figure 4 Regional variation in European green crab claw size and Mytilus mussel shell thickness for four regions. Regional variation in potential determinants of proportion of mussels killed by European green crabs in four regions: BC (British Columbia, Pacific Canada), NS (Nova Scotia, Atlantic Canada), SA (South Africa), and NI (Northern Ireland, UK). (A) Claw size (i.e., propal height, in mm) of crabs, and (B) mussel shell thickness index. Raw data indicated by open circles.

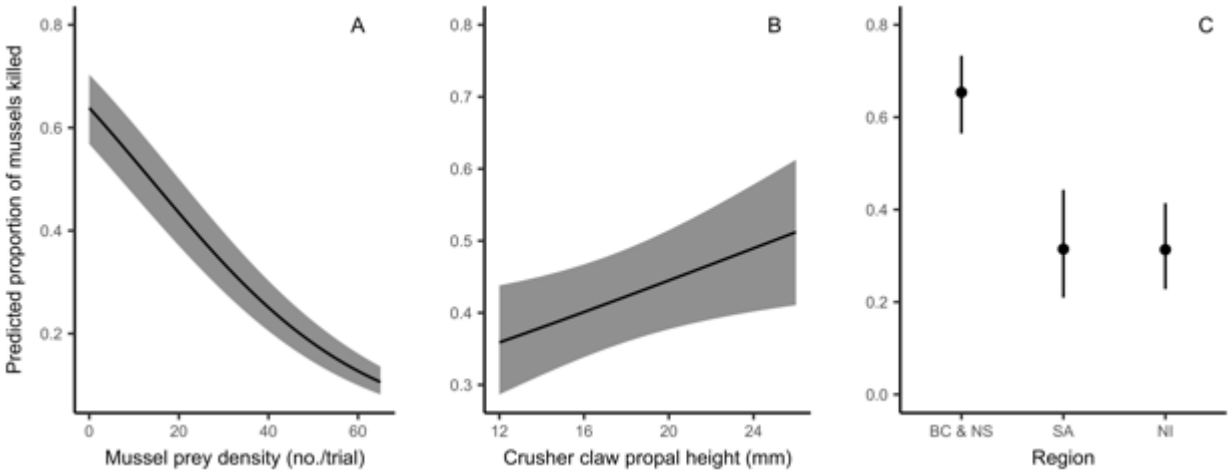

Figure 5 Predicted proportion of mussels killed by European green crabs in relation to prey density, claw size (mm), and the region of origin, derived from top generalized linear mixed-effects model. The predicted proportion of mussels killed by European green crabs (with 95% confidence intervals) in relation to (A) prey density, (B) claw size (mm), and (C) the region from which crabs were collected: North America (British Columbia and Nova Scotia, BC & NS), South Africa (SA), and Northern Ireland, UK (NI). Predictions are derived from a generalized linear mixed-effects model (see top model in Table 1), and are shown for each factor when the other factors are fixed at their mean or proportional values.